RESEARCH PAPER

Aggregate patterns of macrofaunal diversity: An interocean comparison

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Editor: Sally Keith

Funding information
Programa Pesquisador Visitante Especial, Grant Number: 88881.030807/2013-01; CSIC-Grupos Uruguay

Abstract

Aim: While geographical patterns of species richness are reasonably well explored for single well-studied taxa, less is known about aggregate patterns of total richness for major biomes and their environmental correlates. Here we analyse continental-scale aggregate patterns of macrofaunal diversity for sandy beaches, a dominant habitat along the Atlantic and Pacific coasts of South America.

Location: South American coastlines.

Time period: Present day (data amassed from studies performed since 1971).

Major taxa studied: Benthic macrofauna, including crustaceans, polychaetes and molluscs.

Methods: We compiled richness information for all macrofaunal groups on 263 sandy beaches in South America using standard criteria. We further matched these data with environmental variables including sea surface temperature (SST), chlorophyll *a*, grain size, beach slope, tide range and various morphometrics. We used generalized linear mixed models to relate environmental factors to observed variation in total macrofaunal richness across all beaches, testing competing hypotheses about environmental correlates and possible drivers of latitudinal diversity.

Results: Macrofaunal richness decreased from tropical to temperate beaches in the Pacific and followed a parabolic trend in the Atlantic, with the highest biodiversity found at tropical and mid-latitudinal bands. Beach slope, tidal range and chlorophyll *a* mostly explained latitudinal trends in macrofaunal richness, followed by grain size, SST and ocean basin.

Main conclusions: This study indicates that richness of macrofaunal species at a given beach is most closely related to characteristics of the physical habitat, such as beach slope, area and grain size. At this scale, planktonic food supply also appeared to be more important than temperature, which is a dominant explanatory variable of global-scale variation in species richness.

KEYWORDS

benthic macrofauna, environmental correlates, latitudinal diversity, macroecology, sandy beaches, South America

1 | INTRODUCTION

Striking non-random latitudinal patterns in diversity on land and in the ocean have been a major research topic in ecology and biogeography (Hillebrand, 2004; Gaston, 2000; Rohde, 1992). While monotonic

increases in species richness are observed for vertebrates and plants on land (Belmaker & Jetz, 2011; Kreft & Jetz, 2007), marine species groups can show more varied patterns, including subtropical or temperate peaks in diversity (Tittensor et al., 2010; Woolley et al., 2016). Yet the majority of studies have focused on single taxa, while aggregate

patterns of diversity for major habitats or biomes remain less explored (Jetz, McPherson, & Guralnick, 2012). An important reason for this apparent bias towards single, well-known taxa is the difficulty of comprehensively sampling whole faunas, which requires broad taxonomic expertise across well-known and lesser-known groups.

Knowledge of environmental variables can bring us closer to a more mechanistic understanding of geographical diversity patterns, particularly where they relate to ecological theory (Gotelli et al., 2009; Tittensor & Worm, 2016). Previous studies on single taxa have highlighted a large role of ambient thermal energy in explaining patterns of species richness for well-studied coastal and pelagic species groups (Rutherford, D'Hondt, & Prell, 1999; Tittensor et al., 2010; Worm, Sandow, Oschlies, Lotze, & Myers, 2005), supporting the species–energy hypothesis (Allen, Gillooly, & Brown, 2007; Wright, 1983). This hypothesis also predicts patterns of macrofaunal richness in the deep sea, but here a different form of energy (chemical energy exported from surface waters to the deep sea) provides the most consistent environmental variable that explains observed patterns of mollusc (Tittensor, Rex, Stuart, McClain, & Smith, 2011) and ophiuroid diversity (Woolley et al., 2016). Other predictors of diversity are related to habitat characteristics (e.g., coastline length), oceanographic fronts, nutrients and upwelling-related variables, and closeness to continental margins (Fenberg, Menge, Raimondi, & Rivadeneira, 2015; Keith, Kerswell, & Connolly, 2014; Tittensor et al., 2010). Finally, historical differences in the evolution of species richness across ocean basins have been found to be important for some coastal taxa (Tittensor et al., 2010).

Sandy ocean beaches are dynamic environments that make up two-thirds of the world's ice-free coastlines (McLachlan & Brown, 2006). The physical structure of these ecosystems is determined by the interaction between sand, waves and tides (Short, 1999), and resident sandy beach communities are thought to be mainly structured by these distinctive physical features (Defeo & McLachlan, 2005). Global diversity patterns in sandy shores highlight the role of beach morphodynamics and tide range as the main explanatory variables of species richness, which increases towards wide beaches with gentle slopes and fine grains (Barboza & Defeo, 2015; Defeo & McLachlan, 2013). Barboza and Defeo (2015) also highlighted the role of ecoregions, which implicitly include isolation and coastal complexity among other historical geographical factors, and sea surface temperature (SST), as other relevant explanatory variables of global-scale species richness.

Here we have assembled an unprecedented regional dataset on aggregate patterns of species richness for sandy beach macrofauna, drawing on the collective expertise of sandy beach ecologists in South America. The goal of this study was to compare aggregate patterns of diversity across two oceans, the south-western Atlantic and south-eastern Pacific, and to investigate environmental correlates and hypothesized drivers at local to regional scales, using a fine-grained comprehensive coverage not seen in previous global-scale analyses. These study systems offer an interesting contrast due to different regimes in terms of water temperature, productivity and related environmental factors. While the Pacific coast features cold-water currents

and associated upwelling areas, the Atlantic shore features much warmer currents and lower productivity levels (Ortega, Castilla, Espino, Yamashiro, & Defeo, 2012; Thiel, Macaya, & Acuna, 2007). These ocean basins share different ecological and evolutionary histories and harbour distinct faunas with relatively low taxonomic overlap, offering an interesting large-scale contrast for testing major hypotheses about the environmental variables that generated distinct patterns of species richness in the oceans. We analysed richness patterns for whole faunas in a species–energy framework. Specifically, we asked whether thermal energy or productive energy could be the main explanatory variables of species richness, and how habitat characteristics or historical factors play additional roles at the scales examined here.

2 | MATERIAL AND METHODS

2.1 | Database

We collated available information about benthic macrofaunal species richness from Atlantic and Pacific sandy beaches of South America. Using Scopus, ISI Web of Science and JSTOR search engines, we reviewed primary research articles about sandy beaches, collecting information on species richness (defined as the total number of macrofaunal benthic species recorded per survey) and associated environmental variables, where available. The literature review also involved a search of theses and technical reports for sandy beach surveys performed in both continental margins. Manuscripts were assessed and, when available, environmental data and species richness estimates were verified. Following Defeo and McLachlan (2013) and Barboza and Defeo (2015), we considered the following qualifying criteria: (i) only those studies that sampled the entire beach width from the lower swash zone (i.e., water movement over the beach face, after a broken wave collapses on the sand) up to the drift line or above were considered; (ii) subtidal samples were excluded; (iii) where monthly or seasonal surveys were reported, these were pooled to provide a single estimate of species richness for each beach; and (iv) only marine invertebrate macrofauna collected on a sieve of 0.5- to 1.0-mm mesh were considered (McLachlan & Brown, 2006), excluding terrestrial forms such as insects or arachnids. Sandy beach surveys rarely consider the landward distribution of these species and typical sampling devices (e.g., quadrats) are ineffective at capturing highly mobile and flying forms. Unpublished information coming from 62 Brazilian sandy beaches (Cardoso, Skinner and Cabrini, unpublished data) was included in the analysis. The final dataset encompassed 263 sandy beaches (Figure 1a, Table 1): 179 from the Atlantic and 84 from the Pacific (details for each site are found in Table S1 in the Supporting Information), thus covering 16 of the 19 ecoregions defined by Spalding, Fox, and Allen (2007) for the continental coasts of South America. Sandy beach macrofauna mainly comprised crustaceans, molluscs and polychaetes, and the mean ($\pm$ SD) number of species per beach was 12.3 $\pm$ 7.4, ranging from 1 to 37 species (Table 1). A list of the data sources is given in the Appendix.

Data on mean grain size and beach slope, two physical factors that have an outstanding influence on sandy beach macrofauna (Defeo &
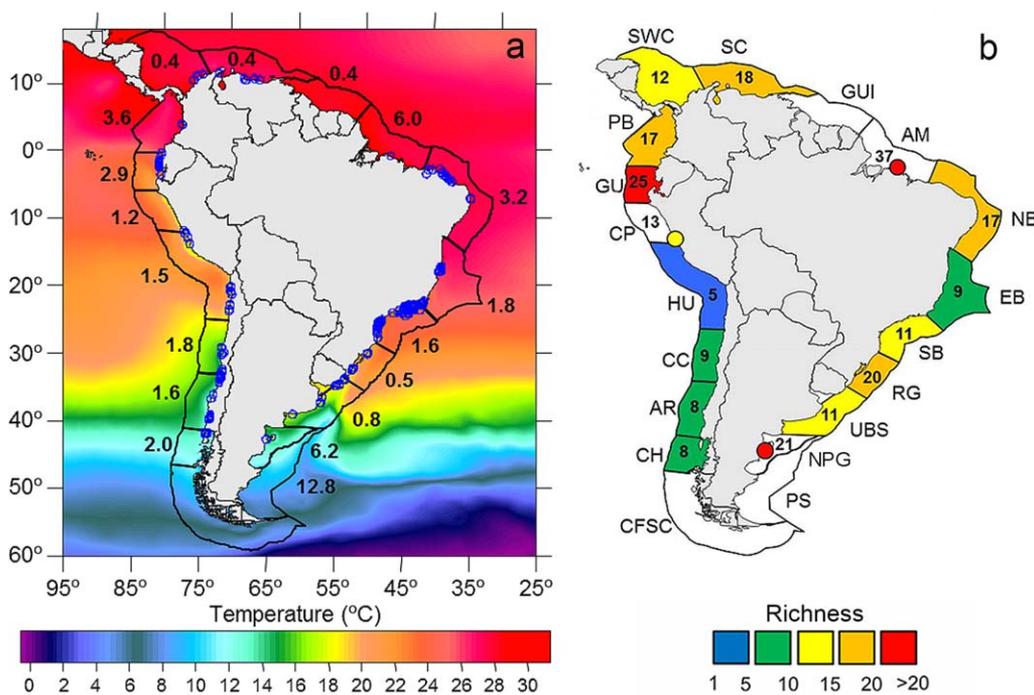
FIGURE 1 (a) Map showing the location of the 263 sandy beaches (blue open circles) included in the analysis and the marine ecoregions defined by Spalding et al. (2007). The satellite image is a mean estimate of sea surface temperature (averaged over the years 2002–14) derived from the Moderate-Resolution Imaging Spectroradiometer (MODIS-Aqua). Mean tidal range estimates extracted from tide tables available for each country and region are shown. (b) Sandy beach species richness (median estimates) in South America, discriminated by marine ecoregion: PS, Patagonian Shelf; NPG, North Patagonian Gulfs; UBS, Uruguay-Buenos Aires Shelf; RG, Rio Grande; SB, South-eastern Brazil; EB, Eastern Brazil; NB, North-eastern Brazil; AM, Amazonia; GUI, Guianan; SC, Southern Caribbean; SWC, South-western Caribbean; PB, Panama Bight; GU, Guayaquil; CP, Central Peru; HU, Humboldtian; CC, Central Chile; AR, Araucanian; CH, Chiloense; CFSC, Channels and Fjords of Southern Chile. A coloured dot was assigned to ecoregions NPG, AM and CP, meaning that only one beach was available for each of these ecoregions

McLachlan, 2013, and references therein), were gathered from all the reviewed articles used to build the dataset. In addition, tidal range was extracted for each beach based on the information contained in tide tables for each country. SST and chlorophyll *a* concentration were also included in the database to test specific predictions generated by the species–energy theory (Clarke & Gaston, 2006). Both variables were obtained from MODIS satellite images available at the Ocean Color website (http://oceancolor.gsfc.nasa.gov). The pixel extraction tool provided by the SeaDAS software was used to extract coastal mean data for the period 2002–14 with a 4-km spatial resolution (see Table 1 for a complete list of environmental variables considered here).

Information on sampling effort was not available for all the sandy beaches under study, hence the relation between sampling effort and species richness was assessed initially using only those 233 sites where such data were made available. No significant relationship between species richness and sampling area was found in a generalized linear model using a Poisson distribution and a log-link function ($n = 233$, estimate $= -0.016$, z value $= -1.197$; p value $= .24$, explained deviance $= 0.16\%$: Fig. S1). These results allowed us to include all sampled beaches in the modelling process.

Two compound indices of beach state were computed: the beach area index (beach area) and the dimensionless fall velocity or Dean's parameter (Ω). Beach area was obtained by dividing the tidal range by

the beach slope, and has been recently used as a proxy for beach width (McLachlan & Dorvlo, 2005) because it represents the distance (in m) along one dimension (from the low- to the high-tide marks). When information on wave height and period was available, Ω was estimated as (Short, 1999)

TABLE 1 Summary statistics of sampled beaches, including observed ranges of biological and environmental variables by ocean

Variable	Atlantic	Pacific
Number of beaches	179	84
SST (°C)	13.5–28.1	13.0–27.5
Chlorophyll *a* (mg·m^{-3})	0.1–21.6	0.7–12.6
Grain size (mm)	0.09–1.18	0.11–0.96
Beach slope (%)	1–19	2–14
Tide range (m)	0.3–6.2	1.0–4.1
Area (m)	5–241	12–177
Ω	0.1–11.7	0.2–10.2
Species richness	1–37	1–35

SST, sea surface temperature.
Not all beaches contained information about the Dean parameter (Ω) detailed in this table.

$$\Omega = \frac{H_b}{W_s \times T}$$

where H_b is breaker height (in m), W_s is sand fall velocity (m·s^{-1}) and T is wave period (s). This index of beach state measures how reflective or dissipative a microtidal beach is. Ω values <2 characterize reflective beaches (narrow, with steep slopes and coarse sands) and Ω values >5 define dissipative beaches (wide intertidal, flat beach slopes and fine sands), with values between 2 and 5 indicating intermediate beach states. When information about a specific physical variable was not available in the papers reviewed, an additional bibliographic search for each sandy beach was performed. However, not all the beaches sampled had all variables available.

2.2 | Statistical analysis

Individual relationships between macrofaunal species richness and latitude, environmental variables or indices of beach state were first evaluated by univariate linear and nonlinear models, discriminated by ocean basin. Generalized linear mixed models (GLMMs) were used to formally determine the relative effect of each environmental variable on sandy beach species richness (Bolker et al., 2009; McCulloch, Searle, & Neuhaus, 2008). The global model was fitted using temperature and chlorophyll *a* as variables relating to the effects of ambient energy (thermal and chemical) on species richness. Key habitat characteristics identified from the univariate analyses and included here were grain size, tidal range and beach face slope. Ocean basin (Pacific, Atlantic) was used to pool variation that might be due to historical differences between oceans not captured by energy- and habitat-related variables. We also included the ecoregions defined by Spalding et al. (2007) as random intercepts (Figure 1a). Ecoregions proved to be informative units in explaining trends in sandy beach species richness at a global scale (Barboza & Defeo, 2015). All other descriptors were included as fixed variables. Collinearity was checked using the variance inflation factor (VIF). VIF values >4 were considered as evidence of collinearity; that is, the information carried by a variable having such a VIF is contained in a subset of remaining variables. The Poisson distribution and a log-link function were used for fitting, taking into account the discrete nature of the response variable (i.e., total number of species). Model parameters were estimated by maximum likelihood by applying the bobyqa optimizer (package optimx; Nash, 2014) using the R statistical computing software (R Development Core Team, 2014).

To avoid the possibility of arbitrary decisions in selecting a single best model, a multimodel inference approach was applied (Burnham & Anderson, 2002). First, all possible candidate models were run using additive combinations (64 of them) of the fixed variables. Corrected Akaike information criterion (AICc), log likelihood scores and AICc weights (AICcw) were estimated in each run and were used for model inference (Burnham & Anderson, 2002). Model weights were used to measure the relative likelihood of a model performing better than all other candidate models, given the data. Models were ranked by AICc values and those with a difference between AICc values (ΔAICc) >4 were excluded from the analyses. Retained models were used to obtain model-averaged parameter estimates and their standard errors. The rel-

ative importance of each variable used for modelling species richness was calculated as the sum of the AICcw over all models in which the variable appears. In this context, variables with an importance <0.3 were considered to have very low influence on predicted values (Burnham & Anderson, 2002). The marginal R^2 (variance explained only by fixed effects) and conditional R^2 (variance explained by fixed and random effects) of the fitted GLMMs were calculated using the R package MuMIn (Barton, 2014). Model validation was performed following the protocol proposed by Zuur, Ieno, Walker, Saveliev, and Smith (2009).

3 | RESULTS

3.1 | Biogeographical trends: Oceans and ecoregions

The highest macrofaunal species richness was found in the tropical Pacific ecoregion Guayaquil (median estimate 25), followed by the temperate Atlantic ecoregion Rio Grande (20), the Atlantic tropical ecoregions Southern Caribbean (18) and North-eastern Brazil (18) and Panama Bight in the Pacific (17) (Figure 1b). It is worth mentioning that the Atlantic ecoregions Amazonia (tropical) and North Patagonian Gulfs (temperate) had high species richness (37 and 21, respectively), but these estimates were derived from only one beach in both cases. No information was available for the Guianas ecoregion because of a marked absence of sandy beaches. Indeed, this ecoregion consists of almost 2000 km of the world's muddiest shores between the mouths of the Amazon (Brazil) and Orinoco (Venezuela) rivers (see Anthony et al., 2010). Large-scale patterns at the province level showed the highest species richness in the tropics (Fig. S2b), specifically the Tropical Eastern Pacific (median estimate: 23 species) and the Tropical North-western Atlantic (18). The tropical North Brazil Shelf Province in the Atlantic presented only one beach with the highest species richness (37).

3.2 | Interocean comparisons

Species richness decreased logarithmically from tropical to temperate beaches in the Pacific, but followed a parabolic trend in the Atlantic, with the highest values found at tropical and temperate latitudes (Figure 2a). For the same latitude, species richness was higher for Atlantic beaches (Figure 2a), which might be related to higher temperatures there (Figure 2b). Species richness linearly increased with SST in the Pacific, whereas in the Atlantic it was lowest at SST values close to 21 °C, increasing towards cooler and warmer waters (Figure 2a and Fig. S3a). The simple univariate representation of the relationship between species richness and covariates, when comparing the Atlantic and Pacific coasts, showed that, with the exceptions of SST (Fig. S3a) and chlorophyll *a* (Fig. S3c), species richness had a very similar response to the physical environment in both oceans. These trends were reinforced by those shown using other composite variables of beach state as continuous descriptors in the between-ocean comparison: species richness consistently increased with beach area (Fig. S3e) and Ω (Fig. S3f). These patterns indicate an increase in species richness with habitat availability and heterogeneity (as denoted by increasing species
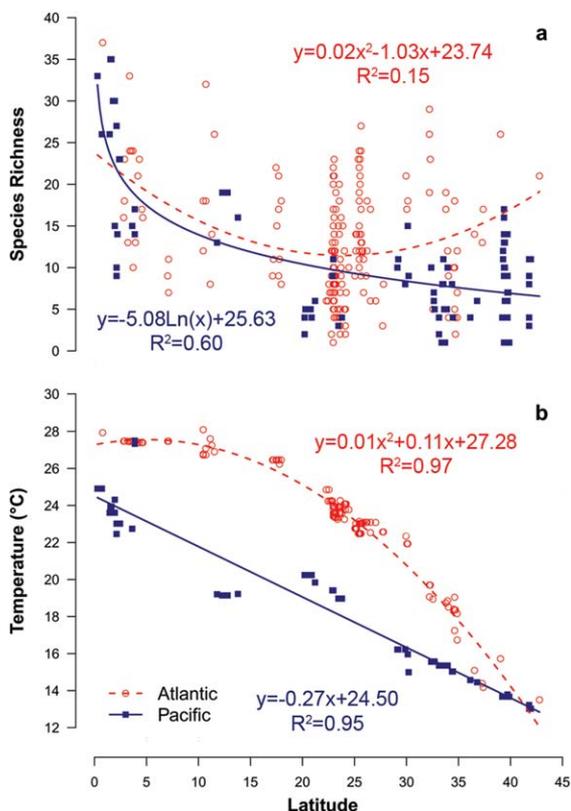
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A Journal of
Macroecology

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FIGURE 2 Latitudinal trends in South American sandy beaches: (a) macrofauna species richness; (b) sea surface temperature. Symbols identify individual beaches in the Atlantic (open circles) and Pacific (squares) Oceans. Regression curves (in all cases $p < .001$) were fitted by least squares

richness with tidal range and beach area) and in ecosystems where wave energy is dissipated throughout the system, reflected by the increase in species richness with Ω, at beaches with flat slopes (Fig. S3b) and fine sands (Fig. S3d). Under extremely reflective conditions, such as found on beaches with very coarse grains, steep slopes and no wave energy, intertidal species were excluded and very few supralittoral forms eventually remained (Table 1, Fig. S3f). This indicates an increase in species richness from microtidal reflective to macrotidal dissipative beaches. In general, the richness of macrobenthic species was higher in the Atlantic than in the Pacific. This pattern was particularly evident when considering beach slope and grain size (Fig. S3b and S3d, respectively) and Ω (Fig. S3f) as covariates.

3.3 | Diversity patterns in South American sandy beaches

Using ecoregion as a random intercept, the best GLMM retained all six variables initially included (Table 2a). Models ranked by AICc values showed that the final GLMM reached an AICc of 1721.3 (Table 2a). The AICcw for the best model was 0.48; that is, this model was the best hypothesis given the data and set of candidate models (Table 2a). The evidence ratio between the first and the second model was 2, providing marginal support for the second, more parsimonious, hypothesis, which excluded ocean basin. Parameter estimates of the best model showed that all variables were statistically significant, except for ocean basin, which was marginally non-significant (Table 2b).

The relative importance of these variables, calculated as the sum of the AICcw over all the models in which each variable appears,
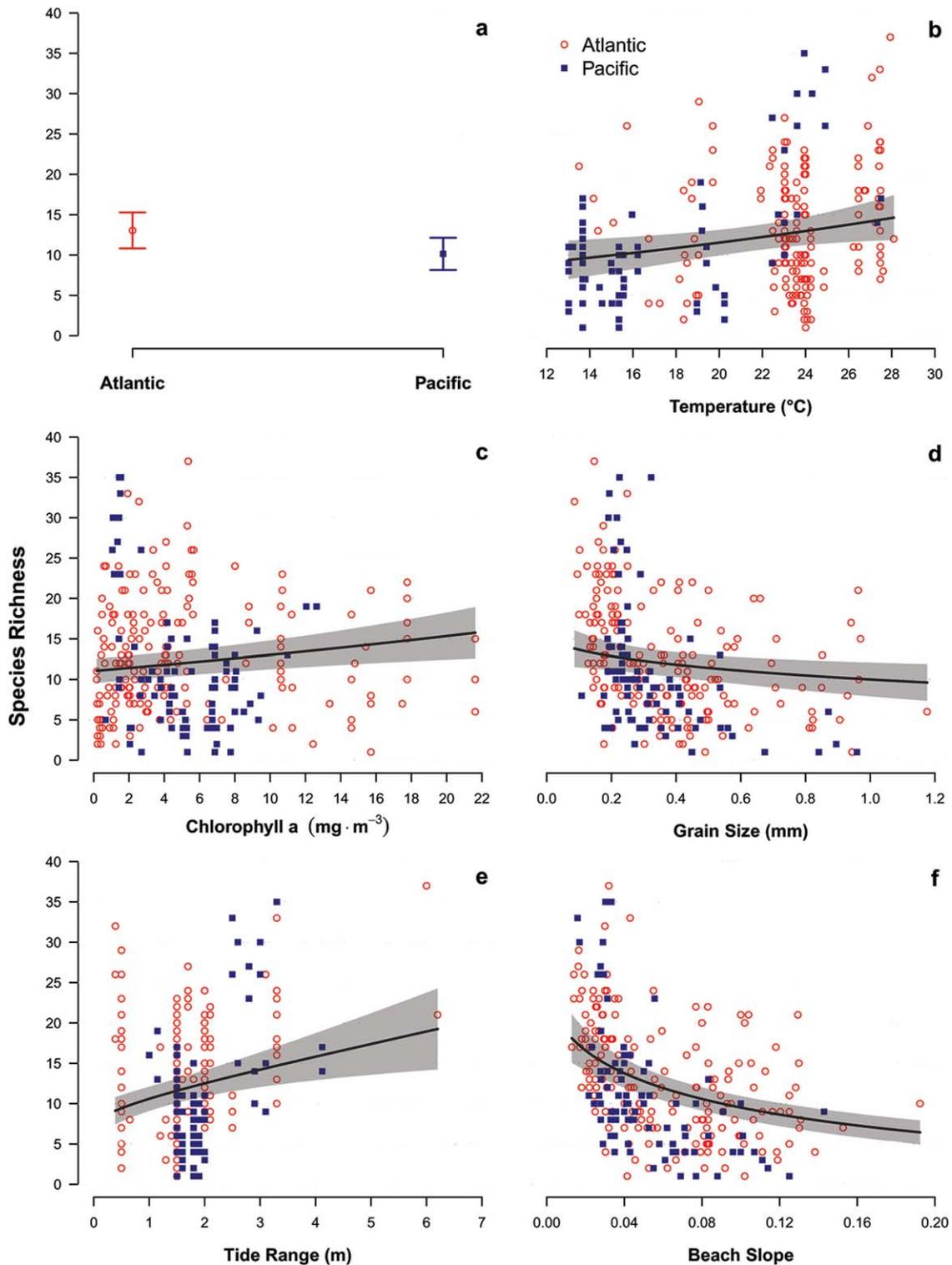
TABLE 2 Generalized linear mixed model relating species richness with key environmental variables for 263 South American sandy beaches

(a) Model selection process								
Candidate models		d.f.	logLik	AICc	ΔAICc	AICcw	R^2_m	R^2_c
Chlorophyll a + *grain size* + *slope* + *tidal range* + *temperature* + *ocean*		*8*	*-852.34*	*1721.3*	*0.00*	*0.48*	*0.39*	*0.49*
Chlorophyll a + grain size + slope + tidal range + temperature		7	−854.08	1722.6	1.34	0.24	0.38	0.47
Chlorophyll a + grain size + slope + tidal range + ocean		7	−854.80	1724.0	2.77	0.12	0.39	0.48
Chlorophyll a + slope + tidal range + temperature + ocean		7	−855.25	1724.9	3.68	0.08	0.31	0.49
(b) Model-averaged coefficients and importance of each variable								
Variables	Estimate	SE	Adjusted SE	z values	p value		Variable Importance	
Slope	−3.236	0.494	0.496	6.530	**<.001**		1.00	
Tide range	0.398	0.099	0.099	4.006	**<.001**		1.00	
Chlorophyll a	0.016	0.008	0.005	3.424	**<.001**		1.00	
Grain size	−0.457	0.190	0.191	2.392	**.020**		0.92	
Temperature	0.032	0.013	0.013	2.546	**.011**		0.87	
Ocean	−0.280	0.149	0.150	1.868	.062		0.73	

d.f., degrees of freedom; logLik, log likelihood scores; AICc, corrected Akaike information criterion; AICcw, AICc weights; R^2_m, marginal R^2; R^2_c, conditional R^2. Models are ordered by AICc values. Only the best models with a difference between AICc values (ΔAICc) <4 are shown. The best model is highlighted in bold and italics.
SE, standard error;
Averaged estimates were calculated using the best models selected through AICc values. Significant p values are highlighted in bold. Environmental variables were not standardized and the coefficient estimates are given on the scale of the link function (log).

FIGURE 3 Generalized linear mixed model relating species richness, environmental variables and ocean basins for 263 sandy beaches from South America: Atlantic (open circles) and Pacific (squares). Mean partial effects of beach slope, grain size, tidal range, temperature, chlorophyll *a* and ocean basins are shown as solid lines with a shaded envelope representing the 95% confidence interval. The marginal and conditional R^2 values of the model were 0.39 and 0.49, respectively

showed that beach slope, tide range and chlorophyll *a* were the most important environmental correlates of species richness, followed by, in decreasing order, grain size, SST and ocean basin (Table 2b). Model results, expressed in the original response variable scale, showed a

decrease of species richness with grain size and slope, and an increase with chlorophyll *a*, tidal range and SST (Figure 3). VIF values ranged between 1.09 and 2.03, confirming the lack of any multicollinearity among variables. The obtained GLMM presented a marginal R^2 of 0.39

and a conditional R^2 of 0.49. Diagnostic plots of model residuals against each environmental variable (Fig. S4) and the relationship between predicted and observed species richness values (Fig. S5) indicated the adequacy of the final model.

4 | DISCUSSION

Using a unique dataset spanning thousands of kilometres for the Atlantic and Pacific sandy beaches of South America, this work showed the concurrent role of individual habitat features (slope, tidal range and grain size) and ambient energy (chlorophyll *a* and SST) in explaining diversity patterns at local to regional scales. Habitat and productivity characteristics, specifically beach slope, tidal range and chlorophyll *a*, were the most important environmental correlates of macrofaunal richness, followed by grain size, SST and ocean basin. Our analysis provides new insights into the ecological processes underlying trends in aggregate species richness at the land–sea interface. Our comprehensive coverage allowed us to test hypotheses at the continental, regional and local levels and to evaluate the existence of latitudinal gradients of richness on Atlantic and Pacific coasts, characterized by different SST and productivity regimes. Our analysis broadly supports global-scale studies (Barboza & Defeo, 2015; Defeo & McLachlan, 2013) that identified local habitat features as overall descriptors of biogeographical structure, but contrasts in highlighting productivity over temperature as a leading environmental correlate, reinforcing the notion of scale dependence in ecology (McGill, 2010).

Primary productivity (here approximated by chlorophyll *a* concentration) was identified for the first time as a key explanatory variable in structuring biogeographical patterns in sandy beach ecosystems. Species richness was positively correlated with chlorophyll *a*, which was more important than SST, in contrast to other coastal taxa (Belanger et al., 2012; Tittensor et al., 2010) but similar to deep-sea invertebrates (Woolley et al., 2016). More productive sandy beaches appeared to promote the coexistence of a larger number of species, thus supporting the productivity–richness hypothesis (Evans, Warren, & Gaston, 2005; Jetz, Kreft, Ceballos, & Mutke, 2009), at least at the local to regional scales examined here. Fenberg et al. (2015) also found that upwelling-related variables, including nutrient concentration and SST, best explained the biogeographical structure of north-east Pacific rocky intertidal species. On many sandy beaches, upwelling and increased wave energy can promote the accumulation of stranded seagrass or algae, and contribute to an increase in local productivity (McLachlan & Brown, 2006). This trend was noticeable in the temperate Atlantic (Rio Grande ecoregion; Figures 1b and 2a), where high wave energy creates hundreds of kilometres of dissipative beaches (gentle slopes and fine grain sizes) characterized by high biomass accumulation of diatoms in their surf zones (Odebrecht, Du Preez, Abreu, & Campbell, 2014). These beaches are particularly lengthy, a critical feature promoting the retention of diatoms in the surf zones of over 50 sandy beaches around the world where these accumulations have been reported (Odebrecht et al., 2014), including the Atlantic sandy beaches of South America analysed here (Fig. S6). The high primary productivity of these

beaches provides a large amount of food, particularly for suspension feeders, and therefore could explain the significantly higher species richness compared with their Pacific counterparts for the same latitudinal band (Figures 1b, 2a and 3a). Surf diatom accumulations have not been reported in Pacific sandy beaches of South America (Odebrecht et al., 2014). In this ocean, the upwelling of cold subsurface waters in the Humboldt Current System causes a weak north–south temperature gradient and extends the influence of cold environmental conditions northward (Thiel et al., 2007). Therefore, sandy beaches from temperate Pacific ecoregions had a small number of macrofaunal species adapted to moderately constant low water temperatures and exhibiting broad distributional ranges (Thiel et al., 2007).

Species richness showed a significant positive relationship with tidal range (which determines the dimension of the intertidal habitat in sandy shores), supporting the hypothesis that habitat availability influences species richness in these ecosystems. Large tidal ranges widen beaches and modify their intertidal profile, increasing habitat heterogeneity and availability for macrofaunal species (see Fig. S3e). Concurrently with tidal range, beach slope correlated strongly with species richness, reinforcing the habitat availability hypothesis. Beach slope is a product of the interaction among wave energy, tidal range and grain size, and therefore large tidal ranges and gentle slopes together are expected to increase the area available for macrofaunal settlement, supporting richer biodiversity. This hypothesis is also reinforced by the clear increase in species richness in Atlantic and Pacific Ocean beaches as a function of beach area (Fig. S3e). Beaches with larger areas also support larger populations (Defeo & McLachlan 2013), thus reducing the probability of species extirpations (MacArthur & Wilson, 1967; Tittensor & Worm, 2016). These patterns, taken together, mean that habitat availability is of utmost importance in explaining local to regional variations in sandy beach diversity patterns. The fact that in both oceans species richness decreased exponentially towards reflective beaches characterized by steep slopes (Fig. S3b) and coarse grains (Fig. S3d) is also in line with the swash exclusion hypothesis proposed for sandy beach ecosystems, which predicts a decrease in species richness from dissipative to reflective beaches (Barboza & Defeo, 2015; Defeo & McLachlan, 2013). Moreover, the similar trends documented for both ocean coasts consistently support the stress hypothesis, which predicts a negative relationship between richness and environmental stress (Fraser & Currie, 1996). Mechanistic explanations for these patterns are related to the turbulent hydrodynamic regimes in swash zones of harsh reflective beaches, which generate abrasive effects on intertidal species, thereby reducing their feeding times, increasing their investment in maintenance and determining lower fecundity and higher mortality rates in comparison with dissipative beach populations (Defeo & McLachlan, 2005). In addition, reflective beaches are low-productivity interfaces subsidized by organic inputs from the sea (McLachlan & Brown, 2006).

SST, which is the only environmental variable that has been consistently identified as an important descriptor of marine species richness across different taxa at a global scale (Belanger et al., 2012; Tittensor et al., 2010), was a meaningful explanatory variable of local to regional

biodiversity patterns in our study. This gives empirical support to the kinetic energy or temperature hypothesis (Clarke & Gaston, 2006; Currie et al., 2004), which predicts a positive correlation between species richness and temperature. Several underlying mechanisms have been hypothesized, including the effect of temperature on community turnover and speciation rates, and an increase in metabolic rates (Tittensor & Worm, 2016).

Deconstruction of the patterns by ocean led to a more complete understanding of the relative contribution of environmental variables to macrofaunal diversity. Species richness was higher in Atlantic than in Pacific sandy beaches (Figure 3a) and distinct macroecological patterns were found between oceans (Figure 2a). Pacific beaches showed a monotonic increase in species richness from temperate to tropical sandy beaches, which could be explained by the concurrent increase in tidal range (Figure 1a) and SST (Figure 2a) towards low latitudes. Rivadeneira et al. (2015) also showed that species richness of rocky intertidal gastropods in the eastern Pacific is elevated up to eight-fold in the tropics compared with extratropical provinces, being also remarkably invariant across temperate provinces in both the Northern and Southern Hemispheres. Thus, the gradient observed for Pacific sandy shores could emerge from the combined effects of species–area and species–energy theory (Tittensor & Worm, 2016), supporting empirical syntheses that invoke temperature and area as general environmental correlates of diversity (Jetz & Fine, 2012; Kreft & Jetz, 2007; Tittensor et al., 2010). Our findings also provide empirical support for recent modelling approaches that highlight the concurrent role of increasing habitat area and thermal effects on speciation rate towards the equator as the main explanatory factors of the latitudinal diversity gradients observed in several faunistic groups (Tittensor & Worm, 2016). Variations in fish species richness across individual estuaries world-wide likewise showed that ambient energy variables (SST and terrestrial net primary productivity) are critical at larger scales, whereas habitat characteristics (estuary area and continental shelf width) are important correlates of species richness at a smaller scale (Vasconcelos et al., 2015).

More complex patterns were found in Atlantic beaches, where species richness was highest at tropical and mid-latitudinal bands. Tidal range, a critical proxy for habitat availability, also had two peaks (Figure 1a): (i) at the tropical North-eastern Brazil and Amazonian ecoregions; and (ii) at temperate North Patagonian gulfs (Figure 1b). Therefore, temperature and area acting together could be explanatory variables of diversity only for the former two tropical ecoregions, but cannot explain the high species richness found in microtidal sandy beaches at the tropical Southern Caribbean ecoregion and at the temperate Rio Grande ecoregion, both with tidal ranges close to 0.5 m. Peaks of temperature and productivity are spatially separated in the Atlantic Ocean, allowing a good discrimination of the kinetic energy or temperature hypothesis and the potential energy or 'productivity–richness' hypothesis. High kinetic energy appears to be facilitating greater species richness in the Caribbean ecoregion, where factors related to available habitat and productivity were of less importance. By contrast, the high productivity in sandy

beaches at the Rio Grande ecoregion (see above and Fig. S6) emerged as the primary environmental correlate of diversity. South-eastern Brazil is also a high-productivity ecoregion characterized by summer shelf break coastal upwellings of cold waters (Ortega et al., 2012; Fig. S6), but the predominance of reflective beaches explains the relatively low species richness found there. Large-scale discontinuities in habitat quality and availability could also explain latitudinal patterns in species richness in Atlantic beaches. In the Atlantic North Brazil Shelf province, particularly in the Amazonian ecoregion, the sediment discharge of the Amazon and Orinoco Rivers largely eliminates sandy beaches and forms the longest predominantly muddy coastline in the world (Anthony et al., 2010).

The strong implications of geographical discontinuities for diversity patterns suggest that geological and evolutionary histories could be important explanatory factors for coastal diversity patterns in sandy shores. This was shown in our study through the explicit consideration of oceanic basins and ecoregions in the modelling process. Concerning the former, the Atlantic has a trailing edge coast with wide sandy beaches, a nearshore zone and a gently sloping inner continental shelf. By contrast, the Pacific is a collision coast with discontinuous beaches with bedrock headlands and a steep and narrow nearshore zone (Davis, 2015). These contrasting features could explain the higher occurrence of dissipative beaches on Atlantic coasts (Fig. S3f) and therefore the higher species richness. The inclusion of ecoregions accounted for differences in coastal habitats and their individual histories, not captured by other variables included in our analysis. The ecoregion scale also captures the approximate regional scale at which biological processes operate in sandy beach macrofauna, which generally have a reduced dispersal, favouring isolation among ecoregions (Barboza & Defeo, 2015). We used spatially structured random intercepts in our modelling approach to capture any dependence among beaches within ecoregions that would not be accounted for by the chosen environmental variables. Other modelling approaches might achieve the same goal, such as the geographically weighted regression used by Keith et al. (2014). Comparing those approaches in view of their assumptions and outcomes would be an interesting methodological question for future work.

In conclusion, our unique coverage of hundreds of sandy beaches at the continental scale provides a new level of understanding of the latitudinal diversity patterns in sandy beach macrofauna. Our hypothesis-driven analyses highlighted the relative contribution of the main explanatory variables of latitudinal patterns in South American sandy beaches, and also tested the strength and direction of large-scale diversity gradients on both ocean coasts. Macrobenthic communities on sandy beaches were mainly associated with both regional ambient energy variables (SST and productivity) superimposed on local conditions in morphodynamic habitat characteristics (tidal range, slope and grain size). System productivity appeared to be more important than SST at this scale, in contrast to what has been shown at global scales, where SST effects dominate for shallow-water species (Tittensor et al., 2010), including those on sandy shores (Barboza & Defeo, 2015). We hypothesize that there is a more general tendency for

diversity patterns to be structured by factors related to habitat and food at local to regional scales, and by temperature at global scales, as shown for land vertebrates (Belmaker & Jetz, 2011). The relative importance of individual environmental factors could be geographically variable, depending on the zone of the beach occupied (Defeo & McLachlan, 2011) and on the type of larval dispersal, as shown for rocky shore invertebrates (Fenberg et al., 2015). By treating different species groups separately and considering their richness at different scales, a more complete understanding of the factors driving species richness patterns may emerge.

Our findings have implications for biodiversity conservation and will allow assessment of changes in sandy beach ecosystem structure and function resulting from changes in the environment. Different lines of evidence suggest that sandy beach macrofauna is reorganizing under the influence of climate change (Ortega, Celentano, Delgado, & Defeo, 2016; Ortega, Celentano, Finkl, & Defeo, 2013). This was reflected in a high sensitivity of macrofauna to increasing SST, sea level rise and erosion of the narrow physical habitat, as well as changes in system productivity (Odebrecht et al., 2014; Ortega et al., 2016). The observed poor faunal adaptive capacity to respond to these changes could be related to sandy beach macrofaunal life-history traits (e.g., ectotherms with reduced motility) and specificity in habitat selection (Defeo et al., 2009). Considering the importance of ambient energy variables (temperature and productivity) and local habitat conditions (slope and tides) as leading correlates of species richness, continued assessment of the effects of climate change should be given a high priority in conservation planning.

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BIOSKETCH

The research group which has collaborated for this article is interested in studying spatio-temporal patterns in biodiversity, their causes and their consequences, in coastal ecosystems around the world.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX : REFERENCES TO DATA SOURCES

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